The Beagle, Records of the Museums and Art Galleries of the Northern Territory, 2008 **24**: 79–86

Juvenile bull sharks *Carcharhinus leucas* (Valenciennes, 1839) in northern Australian rivers

DEAN C. THORBURN AND ANDREW J. ROWLAND

Centre for Fish and Fisheries Research, Murdoch University, South St, Murdoch, Western Australia 6150, AUSTRALIA
Corresponding author: dthorburn@aapt.net.au

ABSTRACT

Juvenile bull sharks, *Carcharhinus leucas*, ranging in total length from 687 mm to 1365 mm, were captured in riverine waters throughout the Northern Territory and Kimberley region, Western Australia. *Carcharhinus leucas* was captured in highest abundance in low salinity riverine waters (<5 ppt), however, none were captured in offshore marine waters. The rivers of northern Australia act as nurseries for juvenile *C. leucas* within which individuals remain for approximately four years. Assuming annuli present on vertebrae were laid down annually and a birth size of approximately 700 mm TL, growth estimates suggest that *C. leucas* attains 863 mm TL in its first year, 993 mm TL in its second year, 1118 mm TL in its third year and 1239 mm TL in its fourth year. Stomach content analysis indicated a broad diet with the consumption of large amounts of teleost fishes within those systems, as well as numerous other prey types including terrestrial mammals, aquatic insects and other elasmobranchs.

Keywords: bull shark, nursery area, *Carcharhinus*, river, Kimberley, Northern Territory.

INTRODUCTION

The occurrence of the bull shark *Carcharhinus leucas* in Australian rivers is well documented as it is the only carcharhinid known to penetrate well into freshwater systems for extended periods of time (Whitley 1943; Chubb *et al.* 1979; Merrick and Schmida 1984; Last and Stevens 1994; Allen *et al.* 2002). However, records of the occurrence of *C. leucas* in offshore waters of Australia are rare, a disparity that may be attributed to the confusion of this species with other whalers and in particular with the very similar pigeye shark (*Carcharhinus amboinensis*) (Cliff and Dudley 1991; Last and Stevens 1994).

Although biological data for Australian populations of *C. leucas* are scarce, various aspects of the life history have been studied elsewhere including Lake Nicaragua (Thorson *et al.* 1966; Thorson and Lacy 1982), the Florida Lagoons (Snelson *et al.* 1984), Gulf of Mexico (Branstetter and Stiles 1987) and South Africa (Cliff and Dudley 1991; Wintner *et al.* 2002). These studies indicate that *C. leucas* can remain in freshwater systems for extended periods and often spends a significant part of its juvenile life in upper estuarine and freshwater reaches (Thorson 1972; Snelson *et al.* 1984; Cliff and Dudley 1991). Breeding is thought to occur in offshore marine waters, with females entering estuarine and inshore waters to give birth (Montoya and Thorson 1982; Bishop *et al.* 2001). Length at birth estimates range from 55 to 90 cm total length (Thorson and Lacy 1982; Snelson 1984; Branstetter and Stiles 1987; Cliff and Dudley 1991; Wintner *et al.* 2002).

Despite the marine affinities of *C. leucas*, this species' utilisation of upper riverine reaches has often led to it being included in studies of freshwater elasmobranchs. This was the case during two previous ichthyological surveys that aimed to capture elasmobranchs in fresh waters of northern Australia (Taniuchi *et al.* 1991; Ishihara *et al.* 1991). As a result of these studies and other surveys of riverine waters *C. leucas* has been shown to occupy numerous systems in tropical and warm temperate regions of Australia extending south to Sydney (New South Wales) and Perth (Western Australia) (Chubb *et al.* 1979; Last and Stevens 1994; Bishop *et al.* 2001; Allen *et al.* 2002; Thorburn *et al.* 2003).

In light of the paucity of knowledge on elasmobranchs occurring in estuarine and freshwaters of northern Australia, ichthyological surveys were conducted in the Northern Territory and Kimberley region of Western Australia in 2002 (Thorburn *et al.* 2003) and additionally in the Fitzroy River (Western Australia) throughout 2003 and 2004 (Thorburn *et al.* 2004). During these surveys, *C. leucas* was captured in higher abundance than any other elasmobranch species, and provided an opportunity to: determine the distribution and any broad-scale habitat associations of *C. leucas* in the rivers of the Northern Territory and Kimberley region, Western Australia; and describe the biology, age composition and diet of *C. leucas* occurring within these rivers. Furthermore, this study aimed to test the hypothesis that juveniles of the species utilise rivers of northern Australia as nursery grounds, by satisfying the criteria defined by Heupel *et al.* (2007) that, "(1) sharks are more commonly encountered in the area than other areas; (2) sharks have a tendency to remain or return for extended periods; and (3) the area or habitat is repeatedly used across years".

MATERIALS AND METHODS

Study sites, environmental variables and habitat. One hundred and eighty-six marine, estuarine and freshwater sites were sampled between the Robinson River (NT) and the Fitzroy River (WA) from June 2002 to July 2004 (Fig. 1). The salinity (ppt), temperature (°C), and an estimate of water clarity using a secchi disc (cm) were recorded at each sample site. The depth (m) and tidal movement were also recorded. Notes on the immediate habitat, including predominant sediment type, density of aquatic vegetation types and detritus, riparian vegetation and snag density, were also made.

Sample collection, measurements and field dissection. Sampling was primarily conducted with sinking monofilament gill nets (including 20 m panels of 5, 7.5, 10, 15 and 20 cm stretched mesh) that were set perpendicular to the river bank. All gill net mesh sizes were utilised during daylight hours, however, only the larger meshes were used at night to minimise by-catch. Baited long-lines and handlines were also used. Long-lines were a maximum of 40 m long and contained up to 20 5/0 tuna circle hooks. Each hook was connected to the 500 lb nylon mainline via 0.5 m of 200 lb wire trace. Locally available fish was used as bait. Long-lines were set during the day and night.

Dissections were conducted in the field as soon as practicable after capture to minimise tissue breakdown and further digestion of the gut contents. The total length (TL, mm), sex and weight (W, g) were recorded for each specimen captured. For comparison with other studies which reported in precaudal length (PCL) only, the conversion TL (cm) = (PCL + 9.16) / 0.81 (Branstetter and Stiles 1987) was used.

The stomach and a minimum of six vertebrae from below the first dorsal fin were removed from 51 female and 49 male *C. leucas*. Stomach fullness and contributions were either determined soon after capture or the stomachs were preserved whole in 100% ethanol for later examination. Vertebral samples were stored in 100% ethanol or kept on ice until they could be frozen.

Length-weight, length-frequency and age. A likelihood ratio test (Cerrato 1990) was used to determine if the length-weight relationship was significantly different between the sexes. As no difference appeared to exist the sexes were pooled and the SPSS statistical package used to determine the line of best fit for the relationship. A length-frequency histogram was generated to aid in the identification of size specific cohorts.

Samples of vertebrae were defrosted and placed in 5% sodium hypochlorite solution until free of tissue. The centra were then rinsed thoroughly in water and allowed to dry for several hours. A minimum of two centra from each sample was embedded in resin and a 0.3 mm longitudinal section cut with an Isomet low speed rotary saw. Sections were then mounted on a slide with DePex mounting medium and observed under a dissection microscope with reflected

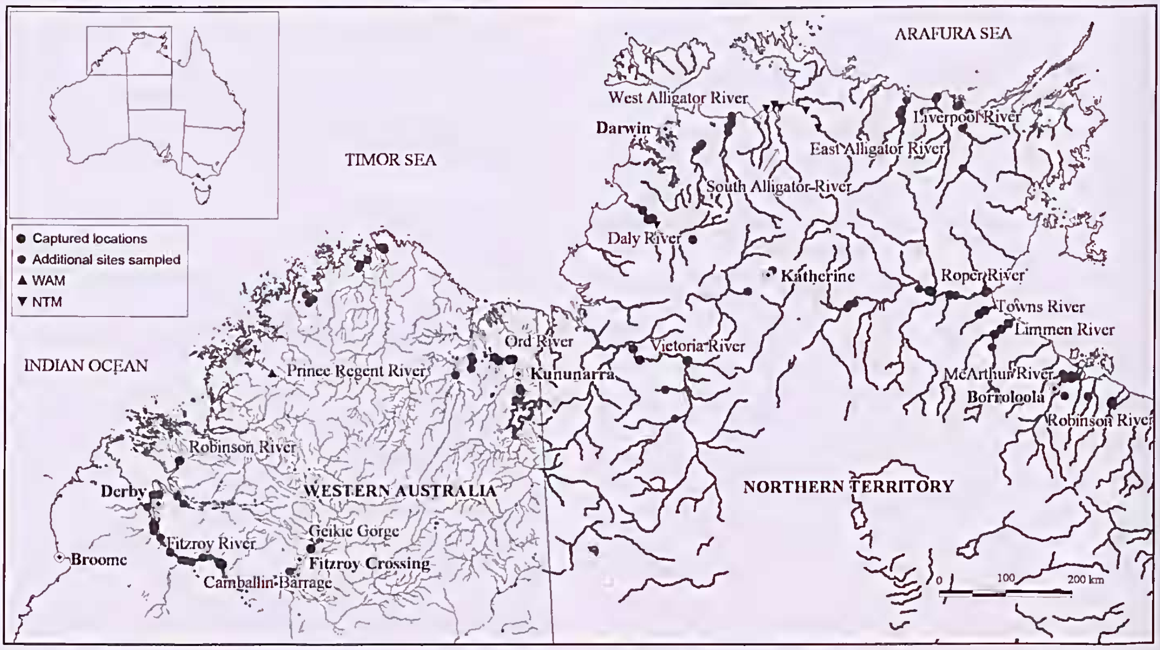

Fig. 1. The sites at which *Carcharhinus leucas* was captured in the Northern Territory and in the Kimberley region of Western Australia. Included are records from the Museum and Art Gallery of the Northern Territory (NTM) and the Western Australian Museum (WAM).

light. Counts of the number of growth rings or annuli commencing after the birth mark (identified by a change of angle on the outer edge of the corpus calcerium) on the facia of whole and sectioned vertebrae were then made for each individual. The number of annuli was compared to TL and the mean size of individuals with respect to the number of annuli calculated. The lack of successive annual samples of vertebrae precluded validation that annuli were laid down annually during the current study. Marginal increment analysis of vertebrae from specimens from the Gulf of Mexico (Branstetter and Stiles 1987) and 'mark-recapture' analysis of captive South African specimens (Wintner *et al.* 2002) confirmed the annual formation of annuli. These findings, in conjunction with fact that length at age and growth rate data collected during the current study (see Results) were comparable to those collected by Branstetter and Stiles (1987) and Wintner *et al.* (2002), suggest that annuli may similarly be laid down annually in Australian specimens.

A von Bertalanffy growth curve was fitted to the length of *C. leucas* at their estimated age of capture, however, this method required the provision of the individual's birth dates. This estimation was subsequently based on the stage of healing of the umbilical scars present on a number of the individuals captured. Healing rates were assumed to be comparable to that of *Carcharhinus cautus* where umbilical scars were observed to be completely healed within three months of birth (Dr William White, CSIRO, Hobart, pers. comm). The birth date of an individual possessing an open umbilical scar was estimated to have been at the beginning of the month of capture. An individual possessing a closed umbilical scar was assumed to have been born at the beginning of the month prior to the date of capture, and an individual possessing a near faded umbilical scar was assumed to have been born two months prior to capture. Other individuals collected from the same river as those possessing umbilical scars, or from other rivers in close proximity, were subsequently assigned the same birth months.

Based on the individuals and times captured, those from (and near to) the Roper River (NT) were assumed to be born 1 June, those from the Daly River (NT) on 1 August, those from the Ord River (WA) on 1 November, and those from the Fitzroy River (WA) on 1 February. A line of regression was fitted with the use of SigmaPlot 8.0 and the von Bertalanffy growth parameters generated by the equation $L_t = L_\infty (1 - e^{-K(t-t_0)})$, where L_t is the length at age t, L_∞ is the mean asymptotic length, K is the growth coefficient and t_0 is the hypothetical age at which the estimated length is zero.

Maturation. Maturation in male *C. leucas* was determined on the basis of clasper calcification. Individuals were considered immature when claspers were small and uncalcified, maturing if claspers were extending and becoming semi-calcified and mature when claspers were fully calcified and sperm was present. Maturity in females was assessed on observations of the ovaries and uteri. Individuals possessing undeveloped ovaries and thin, flaccid uteri were considered immature, maturing when the uterus began to enlarge and ovaries contained differentiated ova, and mature when the ovaries contain yolked ova and an enlarged uterus (Conrath 2004).

Diet. Upon removal of the stomach, an estimate of fullness on a scale of 0 to 10 (zero representing an empty gut and 10 being fully distended) was made. Some smaller prey items required identification under a dissection microscope. An estimation of the percentage contribution of each food item was made for each individual, and the frequency of occurrence (%F) and mean percentage volumetric contribution (%V) calculated (Hynes 1950; Hyslop 1980).

The graphical method of Costello (1990) was also used to display the broad functional prey categories found to constitute the diet of *C. leucas*; %F is plotted against relative quantity (in this case %V). This method takes into account the percentage occurrence, and subsequently provides insight into population wide food habits (Cortes 1997). Unidentified items were excluded from analysis and the values of all other dietary categories of that individual adjusted upward to sum to 100% (Pusey *et al.* 2000). Similar prey categories were combined to reflect a functional prey group.

RESULTS

Capture locations, sex ratio, length ranges and habitat. A total of 111 *C. leucas* were captured from 41 of the 186 sites sampled (Fig.1). Fifty seven were female and 54 were male (sex ratio of 1.06 female : 1 male) which ranged in length from 691 to 1382 mm TL and 687 to 1365 mm TL, respectively (Fig. 2). *Carcharhinus leucas* was only captured within rivers (i.e. upstream of the mouth). The sites of capture ranged in salinity from 0 to 41.1 ppt (Fig. 3), however, 86% of individuals (all of which were

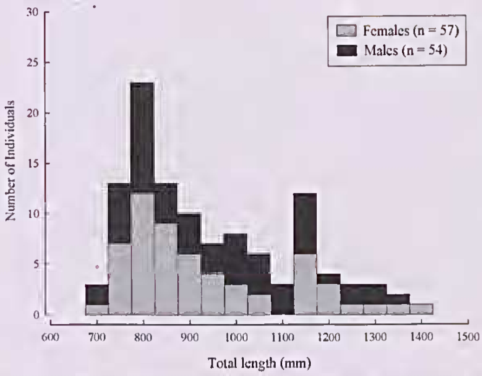

Fig. 2. Length-frequency histogram for female and male *Carcharhinus leucas* collected during the study.

immature) were captured in waters of less than 5 ppt (32% were captured in 0 ppt). *Carcharhinus leucas* was caught in waters ranging in temperature from 20.8 to 32.5 °C that were between 0.7 and 21 m deep and which varied greatly in clarity (5–400 cm secchi depth). The species was generally captured in open waters over sandy substrates that supported low macrophyte and algal growth.

Length-weight relationship, age and growth, maturity and diet. Weights of *C. leucas* ranged from 2360 to 20 500 g in females and from 1740 to 18 000 g in males (Fig. 4). The relationship between TL and W can be described by the formula W = 6165.14 – (21.741TL) + ($0.0228TL^2$).

Observations of the annuli present on the vertebrae of 100 individuals suggested the presence of five year classes (0+ to 4+) (Fig. 5). The average TL of individuals possessing zero annuli on vertebrae was 787 mm, individuals possessing one annuli on vertebrae averaged 859 mm, individuals possessing two annulus on vertebrae

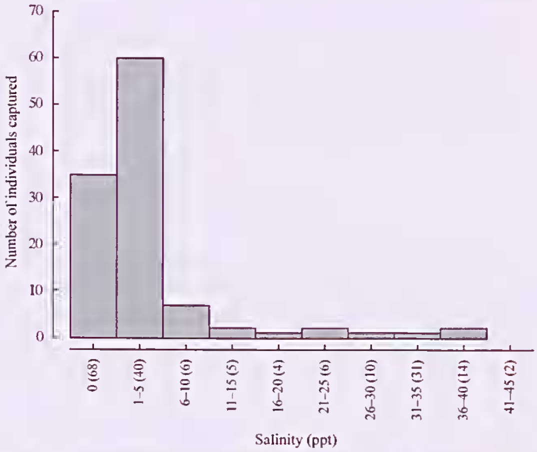

Fig. 3. The number of *Carcharhinus leucas* captured versus sample site salinity (the number of sites sampled are given in parenthesis).

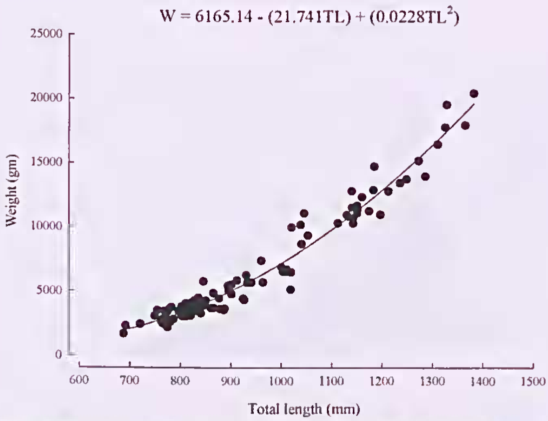

Fig. 4. The relationship between total length (TL) (mm) and weight (W) (g) of *Carcharhinus leucas* captured in northern Australia.

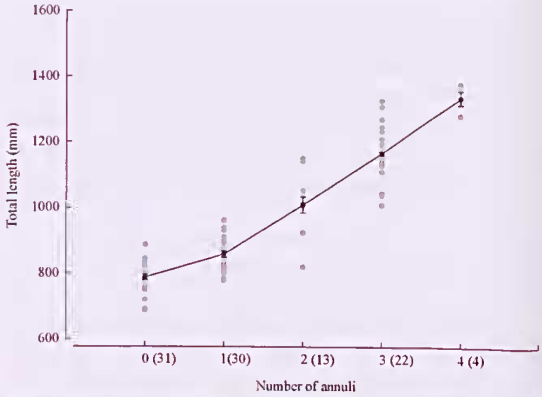

Fig. 5. Number of annuli observed on vertebrae versus the total length (TL) of *Carcharhinus leucas*. The number of individuals possessing 0 to 4 annuli are given in parentheses.

averaged 1010 mm, individuals possessing three annuli on vertebrae averaged 1168 mm and individuals possessing four annuli on vertebrae averaged 1339 mm.

The von Bertalanffy growth equation generated parameter estimates of L_∞ = 4662 mm, K = 0.0347 and t_0 = -4.88 years (Fig. 6). While the L_∞ is above the known maximum size of ~3400 mm TL (Last and Stevens 1994), both the t_0 and L_∞ are comparable to those published for this species elsewhere. From this equation it is estimated that *C. leucas* attains 863 mm TL in its first year, 993 mm TL in its second year, 1118 mm TL in its third year and 1239 mm TL in its fourth year.

All 49 male *C. leucas* captured possessed small non-calcified claspers indicating immaturity. Similarly all 51 females dissected were found to be immature by the possession of undeveloped ovaries and thin, flaccid uteri.

Seventy-six of the 100 stomachs inspected contained prey. Teleost fishes were the major constituents of the diet of *C. leucas* (Table 1, Fig. 7). Where identification of teleost prey to species was possible, the lesser salmon catfish *Ariopsis graeffei*, bony bream *Nematalosa erebi* and scaly croaker *Nibea squamosa* were the major components

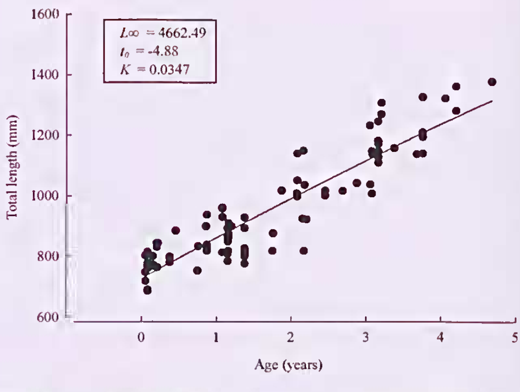

Fig. 6. von Bertalanffy growth curve for *Carcharhinus leucas* collected during the study.

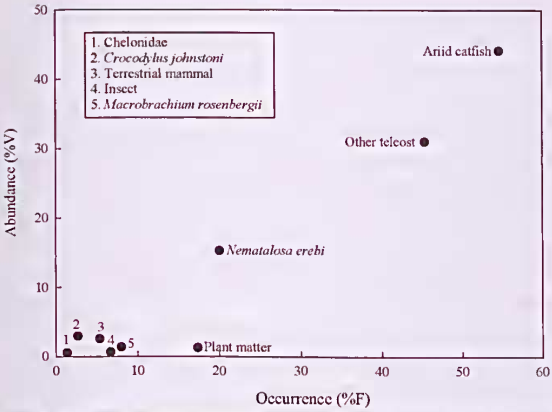

Fig. 7. The important broad functional prey categories of *Carcharhinus leucas*.

Table 1. Percentage volumetric contribution (%V) and percentage occurrence (%F) of the different food items found in the stomachs of *Carcharhinus leucas*.

Prey Item	% V	%F
Vegetation		
Terrestrial vegetation	1.04	13.16
Aquatic macrophyte	0.22	3.95
Macrocrustacea		
Macrobrachium rosenbergii	1.40	7.89
Insect		
Orthoptera	0.03	1.32
Coleoptera	0.63	5.26
Teleost		
Ariopsis graeffei	26.71	32.89
Ariopsis midgleyi	2.41	1.32
Hemiarius dioctes	3.56	2.63
Plicofollis argypleuron	1.27	1.32
Other ariid sp.	10.11	17.11
Harpadon translucens	1.22	1.32
Hemiramphidae (garfish)	0.20	1.32
Lates calcarifer	3.21	5.26
Liza tade	2.08	2.63
Nematalosa erebi	15.14	19.74
Nibea squamosa	9.44	7.89
Polydactylus macrochir	2.86	1.32
Rhinomugil nasutus	0.95	2.63
Scleropluges jardinii	1.26	1.32
Unidentified teleost parts	6.77	21.05
Elasmobranchii		
Pristis microdon	2.54	1.32
Mammal		
Pig	1.59	2.63
Other	0.98	2.63
Reptile		
Chelonidae	0.54	1.32
Crocodylus johnstoni	2.96	2.63
Unidentified	0.89	3.95

of the diet. The removal of the 'unidentified' prey category and consolidation into broad (functional) prey categories further reflected the dominance of teleost species in the diet of *C. leucas*.

DISCUSSION

Distribution and habitat. *Carcharhinus leucas* was frequently captured in fresh waters several hundred kilometres from the coast. The notion that northern Australian rivers act as nurseries for juveniles of the species is strongly supported, and satisfies the definition criteria defined by Heupel *et al.* (2007) in that: high abundances were encountered upstream of the rivers mouths while none were captured from marine waters; all specimens were small and immature and appeared to remain in the river until approximately three or four years of age (assuming annuli were laid down annually); and juveniles of less than one year were captured from the Fitzroy River in each of the three consecutive years of sampling.

Saline estuarine waters have generally been considered to provide important nursery habitats of *C. leucas* more so than freshwaters (Simpfendorfer 2005). During the current study however, the highest abundances of individuals were captured in low salinity waters near the tidal limit and in non-tidal freshwaters, suggesting that in Australia low salinity waters are more important as nursery habitats than higher salinity waters associated with the lower estuary.

The use of upstream waters by juvenile *C. leucas* is likely attributed to the high abundance of food resources available and lack of predators including large sharks and estuarine crocodiles *Crocodylus porosus* (Simpfendorfer and Milward 1993; Morgan *et al.* 2004). Upstream migration of the species was demonstrated on several occasions where the highest abundances of individuals were encountered immediately below a barrier such as an exposed rock bar, road crossing or barrage. In a number of cases, these barriers also represent the upper limit of tidal influence and may partially explain the high abundance of this species in those reaches.

Size and age structure of *C. leucas* in northern Australian rivers. The structure of riverine populations in northern Australia appears similar to those observed elsewhere including North America where *C. leucas* resides in inland waters of the Florida Lagoons for a similar period of time (Snelson *et al.* 1984). Studies by Wintner *et al.* (2002) and Cliff and Dudley (1991) suggested that *C. leucas* in South Africa are born slightly larger than elsewhere, including the coastal lagoons of Florida, Nicaragua and the Gulf of Mexico, i.e. 800 to 900 mm TL cf. 600 and 750 mm TL, respectively (Snelson *et al.* 1984; Thorson and Lacy 1966; Branstetter and Stiles 1987). During the current study, open umbilical scars were observed on individuals between 687 and 749 mm TL. The size at birth of Australian *C. leucas* was therefore found to be comparable to individuals of the latter locations.

Umbilical scars were observed in individuals captured from the Roper River (NT) in June, Daly River (NT) in August, Ord River in November (WA) and from the Fitzroy River (WA) in February. Bishop *et al.* (2001) suggests that *C. leucas* in Australia are born during summer which coincides with the early portion of the tropical wet season. This apparent westward progression of birthing across northern Australia may therefore be a response to the westward onset of the wet season (considered to be between October and April in the NT and between January and March in WA) (Bureau of Meteorology, Commonwealth of Australia 2004). High river discharges associated with the wet season subsequently provide the opportunity for juvenile *C. leucas* to penetrate far upstream before the contraction of water levels during the tropical the dry season.

Various studies have indicated that the annual growth rate of *C. leucas* is greatest in the first few years of life (Caillouet 1969; Thorson and Lacy 1982; Branstetter and Stiles 1987; Wintner *et al.* 2002). Assuming that annuli were laid down annually, length at age estimates generated during this study of 863 mm TL at one year of age and 1239 mm TL at four years of age are consistent with those observed from the Gulf of Mexico (Branstetter and Stiles 1987). However, length at age estimates of northern Australian specimens appear lower than those from South Africa where a one year old *C. leucas* was estimated to be 1040 mm TL and a four year old estimated to be 1406 mm TL (Wintner *et al.* 2002). The current study also estimated that annual growth in the first four years may be approximately 135 mm yr^{-1}. This annual growth estimate is marginally greater than that observed in South Africa (an average of 110 mm yr^{-1} in the first three years) (Wintner *et al.* 2002), however, it is less than the growth rate observed in Nicaragua (an average of 160 – 180 mm yr^{-1} in the first two years) (Thorson and Lacy 1982) and the Gulf of Mexico (an average of 150 – 200 mm yr^{-1} for the first 5 years) (Branstetter and Stiles 1987).

Occurrences of sharks greater than two metres in length were reported from near Fitzroy Crossing on the Fitzroy River (Western Australia) over 300 km upstream of the mouth. Furthermore, the senior author observed a *C. leucas* of approximately two metres TL swimming immediately below Camballin Barrage approximately 150 km from the mouth of the Fitzroy River. Based on the von Bertalanffy growth equation and length weight relationship for younger *C. leucas* generated during this study, these specimens would be 11 years old and weigh 54 kg. Size of maturity data collected from elsewhere has indicated that *C. leucas* attains sexual maturity at between 1600 and 2200 mm TL in males and between 1800 and 2250 mm TL in females (Thorson *et al.* 1966; Bass 1977; Branstetter and Stiles

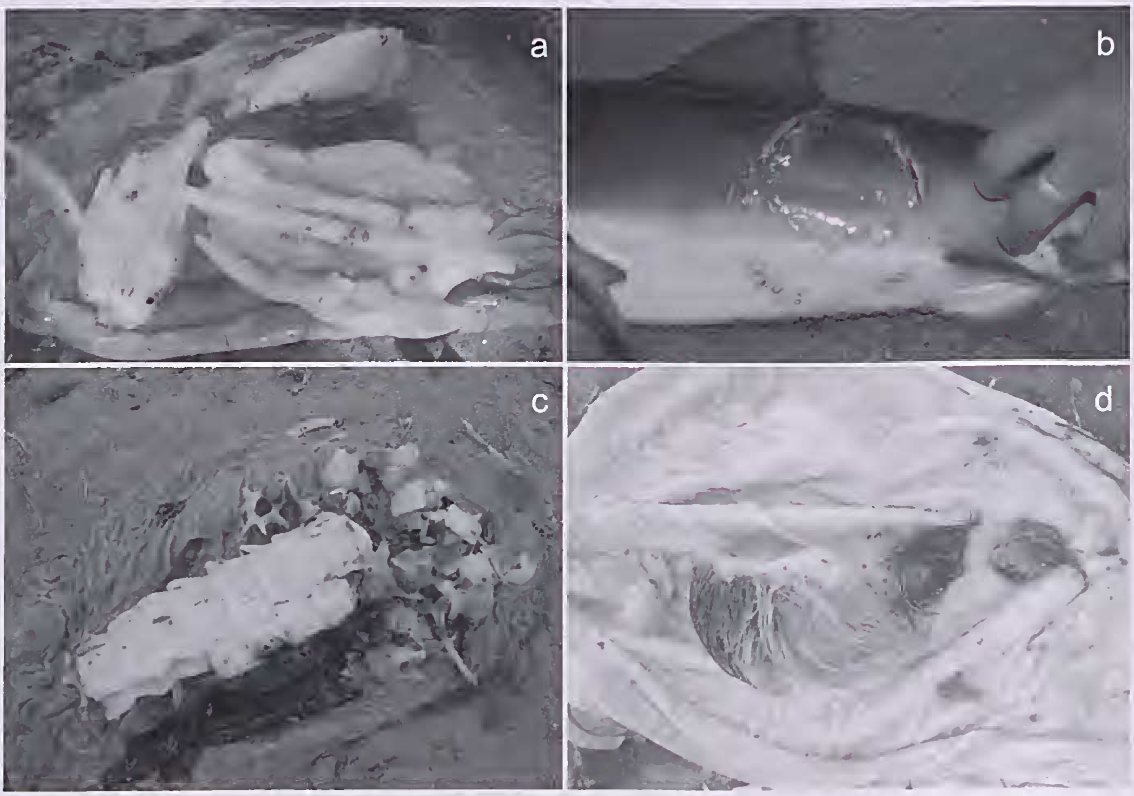

Fig. 8. Stomach contents and potential prey of *C. leucas*, including (a) freshwater sawfish *Pristis microdon*, (b) other *C. leucas*, (c) freshwater crocodile *Crocodylus johnstoni* and (d) feral pig.

1987; Cliff and Dudley 1991). Based on the aforementioned observations and the length at maturity estimates, the presence of mature *C. leucas* in northern Australian rivers can not be dismissed.

Feeding behaviour and predation. Inspection of the stomach contents of *C. leucas* indicated the consumption of a wide variety of prey types and an opportunistic often indiscriminate hunting pattern. While a vast majority of the diet consisted of bony fishes (in particular ariid catfishes), unusual prey including mammals (pig), other elasmobranchs (*Pristis microdon*) and portions of freshwater crocodiles (*Crocodylus johnstoni*) were observed (Fig. 8). Vegetation (aquatic and terrestrial) was also encountered in a high proportion of the stomachs inspected, further reflecting the random nature of prey selection. The authors were also witness to cannibalism by the species whereby *C. leucas* captured in gill nets were attacked by others. Several *C. leucas* were also observed leaping approximately 2.5 m clear of the water to take birds perched on overhanging branches in the Fitzroy River, Wester Australia.

Anecdotal accounts of aggressive feeding described by traditional owners of the Fitzroy River may also suggest the presence of cooperative hunting behaviours. Of particular interest was an account of an attack on a feral pig that had entered the waters edge to drink. As explained, several small *C. leucas* attacked the legs of the pig and proceeded to pull it into deeper water. The pig eventually drowned and was consumed. An additional report of an attack by *C. leucas* on a freshwater crocodile was also collected. A single *C. leucas* was observed to rapidly disable the crocodile by biting off one of its front legs. Numerous other *C. leucas* subsequently appeared and proceeded to bite the remaining limbs before attacking the body.

ACKNOWLEDGMENTS

Sincere thanks must go to Dr David Morgan, Dr Howard Gill, Dr Peter Last, Dr John Stevens, Dr Helen Larson, Dr Barry Russell, Steven Gregg and family, Stirling Peverell, Dr William White, Michael Taylor and Matt Pember, the Natural Heritage Trust, Murdoch University, Department of Fisheries Government of Western Australia, Northern Territory Fisheries, Museum and Art Gallery of the Northern Territory, Kimberley Land Council and Department of Conservation and Land Management.

REFERENCES

Allen, G. R., Midgley, S. H. and Allen, M. 2002. *Field Guide to the freshwater fishes of Australia*. CSIRO/Western Australian Museum: Perth.

Bass, A. J. 1977. Long-term recoveries of tagged sharks. *Copeia* **3**: 574–575.

Bishop, K. A., Allen, S. A., Pollard, D. A. and Cook, M. G. 2001. *Ecological Studies on the Freshwater Fishes of the Alligator Rivers Region, Northern Territory: Autecology*. Supervising Scientist Report 145, Supervising Scientist: Darwin.

Branstetter, S. and Stiles, R. 1987. Age and growth of the bull shark, Carcharhinus leucas, from the northern Gulf of Mexico. *Environmental Biology of Fishes* **20**: 169–181.

Caillouet, C. W. 1969. Weight, length and sex ratio of immature bull sharks, *Carcharhinus leucas*, from Vermillion Bay, Louisiana. *Copeia* **1**: 196–197.

Cerrato, R. M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 1416–1426.

Chubb, C. F., Hutchins, J. B., Lenanton, R. C. J. and Potter I. C. 1979. An annotated checklist of the fishes of the Swan-Avon river system, Western Australia. *Records of the Western Australian Museum* **8**: 1–55.

Cliff, G. and Dudley, S. F. J. 1991. Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. *South African Journal of Marine Science* **10**: 253–270.

Conrath, C.L. 2004. Reproductive biology. In: Musick, J. A. and Benfil, R. (Eds) *Elasmobranch Fisheries Management Techniques*, APEC Fisheries Working Group. Pp. 133–164.

Cortes, E. 1997. A critical review of methods of studying fish feeding based on stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Science* **54**: 726–738.

Costello, M. J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology* **36**: 261–263.

Ebert. D. A. 2003. *California Natural History Guides. Sharks, Rays and Chimaeras of California*. University of California Press, Berkeley.

Heupel, M. R., Carlson, J. K. and Simpfendorfer, C. A. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* **337**: 287–297.

Hynes, H. B. N. 1950. The food of sticklebacks with a review of the methods used in studies of food in fishes. *Journal of Animal Ecology* **19**: 36–58.

Hyslop, E. J. 1980. Stomach content analysis – A review of methods and their application. *Journal of Fish Biology* **17**: 411–429.

Ishihara, H., Taniuchi, T., Sano, M. and Last, P. R. 1991. Record of *Pristis clavata* Garman from the Pentecost River, Western Australia, with brief notes on its osmoregulation, and comments on the systematics of the Pristidae. *University Museum, University of Tokyo, Nature and Culture* **3**: 43–53.

Last, P. R and Stevens, J. D. 1994. *Sharks and Rays of Australia*. CSIRO Division of Fisheries, CSIRO, Australia.

Merrick, J. R. and Schmida, G. E. 1984. *Australian Freshwater Fishes. Biology and Management*. Griffin Press: Netley, South Australia.

Montoya, R. V. and Thorson, T. B. 1982. The bull shark (Carcharhinus leucas) and largetooth sawfish (*Pristis perotteti*) in Lake Bayano, a tropical man-made impoundment in Panama. *Environmental Biology of Fishes* **7**: 341–347.

Morgan, D. L., Allen, M. G., Bedford, P. and Horstman, M. 2004. Fish fauna of the Fitzroy River in the Kimberley region of Western Australia – including the Bunuba, Gooniyandi, Ngarinyin, Nyikina and Walmajarri Aboriginal names. *Records of the Western Australian Museum* **22**: 147–161.

Pusey, B. J., Read, M. G. and Arthington, A. H. 2000. The dry-season diet of freshwater fishes in monsoonal tropical rivers of Cape York Peninsula, Australia. *Ecology of Freshwater Fishes* **9**: 177–190.

Simpfendorfer, C. A., Freitas, G. G., Wiley, T. R. and Heupel, M. R. 2005. Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. *Estuaries* **28**: 78–85.

Simpfendorfer, C. A. and Milward, N. E. 1993. Utilisation of a tropical nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes* **37**: 337–345.

Snelson, F. F., Mulligan, T. J. and Williams, S. E. 1984. Food habitats, occurrence, and population structure of the bull shark, Carcharhinus leucas, in Florida coastal lagoons. *Bulletin of Marine Science* **34**: 71–80.

Taniuchi, T., Shimizu, M., Sano, M., Baba, O. and Last, P. R. 1991. Description of freshwater elasmobranchs collected from three rivers in northern Australia. *University Museum, University of Tokyo, Nature and Culture* **3**: 11–26.

Thorburn, D. C., Peverell, S., Stevens, J. D., Last, P. R. and Rowland, A. J. 2003. *Status of Freshwater and Estuarine Elasmobranchs in Northern Australia*. Report to the Natural Heritage Trust.

Thorburn, D. C., Morgan, D. L., Rowland, A. J. and Gill, H. S. 2004. *Elasmobranchs in the Fitzroy River, Western Australia*. Report to the Natural Heritage Trust.

Thorson, T. B. 1972. The status of the bull shark, *Carcharhinus leucas*, in the Amazon River. *Copeia* **3**: 601–605.

Thorson, T. B. and Lacy, E. J. 1982. Age, growth and longevity of Carcharhinus leucas estimated from tagging and vertebral rings. *Copeia* **1**: 110–116.

Thorson, T. B., Watson, D. E. and Cowan, C. M. 1966. The status of the freshwater shark of Lake Nicaragua. Copeia **3**: 385–402.

Whitley, G. P. 1943. Ichthyological descriptions and notes. *The Proceedings of the Linnean Society of New South Wales* **68**: 114–144.

Wintner, S. P., Dudley, S. F. J, Kistnasamy, N. and Everett, B. 2002. Age and growth estimates for the Zambezi shark, *Carcharhinus leucas*, from the east coast of South Africa. *Marine and Freshwater Research* **53**: 557–566.

Accepted 15 April 2008